

GENDER-RELATED DIFFERENCES IN GAS EXCHANGE
RATES IN THE GENDER-SWITCHING SPECIES
ARISAEMA TRIPHYLLUM (ARACEAE)

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ABSTRACT. Females in dioecious species are generally expected to have higher rates of photosynthesis than are males of the same species. This sexual dimorphism is believed to evolve to compensate for higher costs of reproduction in females relative to males. However, some studies have shown that males in dioecious species have higher rates of carbon assimilation than females. The current study measures photosynthetic rates in males and females of the same genotype in the gender-switching species, *Arisaema triphyllum*. Males were found to have higher photosynthetic rates on a per unit area basis. However, females had greater overall carbon assimilation rates because of their significantly greater leaf area. Photosynthesis in the current study was measured at flowering; presumably developing embryos were not acting as carbon sinks at this time. *Arisaema triphyllum* has a corm (an underground storage organ) that may be the primary sink for carbon. A regression including only females reveals a significant inverse relationship between pseudostem diameter (a proxy for corm size) and photosynthetic rate; as corm size increased, the photosynthetic rate decreased. This suggests that in very large females having greater stored resources, the corm is not as strong a sink as it is for smaller females, at least during the flowering phase of the growing season. For smaller females however, photosynthetic rates do appear to be sink-limited. There was no relationship between corm size and photosynthetic rates among males. Overall, males and females appear to have different patterns of assimilation, at least early in the growing season.

Key Words: photosynthesis, gender switching, carbon assimilation, sexual dimorphism, *Arisaema triphyllum*, Araceae

Dioecious plant species have male (pollen-bearing) and female (ovule-bearing) reproductive phases on separate individuals. In some species, dioecy is known to be genetically controlled (Barlow and Wiens 1975, 1976; Mulcahy 1967; Schink and Mechelke 1989; Warmke 1946; Westergaard 1946; Ye et al. 1991), while in others, gender expression is labile (Schlessman 1988). Among both dioecious and sexually labile species, females have often

been found to allocate more of their resources to reproduction than males (Clay 1993; Dawson and Ehleringer 1993; Dawson et al. 1990; Gross and Soule 1981; Lloyd and Webb 1977; Lovett Doust et al. 1986).

Greater allocation to reproduction among females is thought to provide evidence of a higher cost of reproduction for females relative to males. This pattern of allocation is consistent with Bateman's principle, which suggests that female reproductive success is limited by resources while male reproductive success is limited by mate availability (Bateman 1948). In response to differential reproductive costs, sexual dimorphism appears to have evolved in many morphological as well as physiological traits. Sexual dimorphism may be found in overall plant size and floral display, in life history traits, and in general patterns of resource allocation to reproduction versus growth and survival. As a result of allocation strategies thought to have evolved in response to higher female reproductive costs, females with high reproductive effort may have lower survival rates than males, may grow more slowly than males, and may have a lower reproductive potential than males following a reproductive episode (Lloyd and Webb 1977).

In addition to tradeoffs in allocation to reproduction versus growth and survival, sexually dimorphic patterns in physiological traits related to carbon acquisition have also been observed. In general, females of dioecious species are thought to have greater inherent photosynthetic rates relative to males of the same species (reviewed in Dawson and Geber 1999; Delph 1999) to compensate for higher reproductive costs. When photosynthesis is sink limited, differences between the assimilation rates of males and females may arise as a result of increased sink strength, driven by maturing fruits, for example (Dawson and Bliss 1989; Delph 1999; Delph and Meagher 1995). In some studies, however, males have been shown to have higher overall rates of photosynthesis than females (Gehring and Monson 1994; Laporte and Delph 1996; Marshall et al. 1993). Moreover, Marshall et al. (1993) found that nonreproductive individuals had the same photosynthetic rates as females. Marshall et al. (1993) suggested that male reproduction may cost more than female reproduction in *Phoradendron juniperinum* Engelm. ex A. Gray because of the abundant pollen production, while Delph and Meagher (1995) suggested that males may have a higher overall carbon cost related

to architectural differences between males and females in *Silene latifolia* Poiret. Although males in *S. latifolia* have nearly twice the dark respiration rate of females, they still fix 50% more carbon than fruiting females (Laporte and Delph 1996). Delph (1999) pointed out that understanding the basis of physiological differences between males and females may be important to understanding relative costs of reproduction.

Gender-changing species such as *Arisaema triphyllum* (L.) Schott, Jack-in-the-pulpit, offer an unusual opportunity for exploring the relationship between gender expression and photosynthetic capacity. Unlike dioecious species that have been studied previously, genotypic differences in photosynthetic capacity can be completely controlled in *A. triphyllum*. In gender-changing species, individuals may exhibit either the male or female phase, usually depending on size. In *A. triphyllum*, nonreproductive individuals are the smallest individuals in a population, while males tend to be intermediate in size and females are always the largest individuals (Bierzychudek 1982, 1984; Ewing and Klein 1982; Lovett Doust and Cavers 1982; Lovett Doust et al. 1986; Policansky 1987; Schaffner 1922; Vitt 1997). In addition, vegetative reproduction is common in natural populations, allowing for comparisons of physiological traits between individuals that differ in gender but not genotype.

While the relative costs of reproduction for males and females of this species remain unknown, *Arisaema triphyllum* has many traits that suggest that reproduction is energetically more expensive during the female phase: females are always larger, on average, than males within the same population (Bierzychudek 1982; Ewing and Klein 1982; Policansky 1987; Vitt 1997); gender in one year has a significant effect on gender in the subsequent year with males more likely to become female than females are to remain female in the next season (Vitt 1997); females that produce fruit are more likely to be male or vegetative in the subsequent season than are females without fruit (Policansky 1987); larger females produce more flowers, fruits, and seeds than smaller females, and successful fruit and seed maturation is positively correlated with plant size (Lovett Doust et al. 1986); females devote a greater portion of dry weight to reproductive structures than do males (Lovett Doust and Cavers 1982); and females have a higher mortality rate than males (Policansky 1987).

The intention of this study was to measure the photosynthetic capacity of both a male and a female ramet of the same genotype to better understand the correlation between photosynthetic rates and gender. I hypothesized that females would have a higher photosynthetic capacity than males of the same genotype because of their potentially greater cost of reproduction. Therefore, I measured full light curves of cloned male and female ramets that had been grown under common garden conditions. Photosynthetic measurements were conducted during flowering when the reproductive costs of the inflorescence were likely to have already been met from stored resources, and males and females were most likely to have similar carbon allocation patterns. At flowering, both males and females are supporting reproductive tissue, and, in females, embryos are not yet providing sinks for photosynthate. As both sink strength and whole-plant carbon acquisition are dependent upon organ size, both leaf size and the diameter of the pseudostem were recorded for each individual included in the study.

MATERIALS AND METHODS

Study species. *Arisaema triphyllum*, like other members of the Araceae, is a self-incompatible, diphasic species (Treiber 1980). The dynamics of the gender changing system have been well-characterized (Bierzychudek 1984; Lovett Doust and Cavers 1982; Policansky 1987), and it has been established that plants are vegetative when small, female when large, and male when intermediate in size. A single genetic individual is capable of expressing either gender or of remaining vegetative. The size and reproductive status of any given individual probably reflects resources obtained in the year prior to expression, and is a manifestation of net carbon gain during the previous year (Vitt 1997). Females generally elaborate two leaves and one inflorescence early in the growing season, while males generally produce only one leaf and a single inflorescence. For the duration of the flowering period, carbon gained from photosynthesis may be allocated to tissue maintenance, developing embryos, or the storage organ. Developing embryos and corms are carbon sinks in females, while only corms act as sinks in males.

Common garden. One hundred newly emerging plants were collected from a very large natural population in Chaplin, Con-

necticut, in May of 1992. Asexual reproduction in this species occurs such that vegetative offshoots are quite closely situated to the parent plant, resulting in usually well-delineated groups of shoots. Only individuals that were a minimum of 3 meters apart were collected to increase the probability of including genetically distinct individuals. Plants were grown in the greenhouse for one year, in 6-inch ceramic pots with an equal mixture of sand, peat, and sterilized loam. The pots were placed on greenhouse tables in random order and were rotated every two weeks. A 75% shade cloth structure was erected above the table to simulate forest understory conditions. Pots were watered once a day, and were fertilized once in the growing season with a weak fertilizer solution. Following leaf senescence, pots were moved into a cold room until the following spring.

Eighty-four plants (genets) were chosen at random from the greenhouse population to be planted in an outdoor common garden plot in May of 1993 at the University of Connecticut Plant Research Station in Mansfield, Connecticut. Each plant was placed randomly in a 30 × 30 cm grid so that each individual was 30 cm from the nearest individuals. Plants were then watered and mulched with 2 inches of cocoa hulls, which are relatively inert. The plants were watered only three more times during that summer, and then only during extended periods of no rain. They were not fertilized. The plot was weeded by hand as necessary to eliminate competitors. In early June of 1993, and in June of each subsequent year through 1995, a shade structure consisting of a double thickness of 50% shade cloth was erected over the entire plot to simulate canopy closure at approximately the time during which it occurred in the natural populations. The shade cloth was removed in November of each year. Gender for 1993 was already established at the time of transplant (Vitt 1997), and all but one of the reproductive individuals were female.

Photosynthetic and morphological measurements. Natural production of clones was exploited to produce genets represented by a male, female, and vegetative ramet. Following a two-year period, however, only seven genets included both a male and a female ramet, and only two of these also had vegetative ramets. The majority of newly cloned ramets expressed gender as male because they were smaller than the parent plant. Light curves for all 7 genotypes with a male and female ramet (a total of 14

individuals) were measured using an LI-6200 portable gas exchange system (LiCor Instruments, Lincoln, NE). All measurements were taken during the first two weeks in June while the plants were flowering. The spring of 1995 was slightly late, and in addition, the common garden was situated on a fairly exposed location. Flowering in the common garden, therefore, was somewhat later than in natural populations.

Two or three light curves were measured per day from 0700 to 1400 hours EST to decrease any time effects. Plants were used for measurement only when the leaves were fully expanded, and the inflorescence was considered to be functional. For males, this required that the anthers were either white or pink in color and were actively shedding pollen. Females were considered functional when the ovaries were green, round in shape, and not swollen. The stigmas had to be white and somewhat glossy in appearance. The plant measured at any given time during the day was chosen arbitrarily from those considered functional to ensure that neither males nor females were measured more often at a particular time of day, nor on a particular day in the sequence of days.

A portion of a single leaflet was enclosed in the Lucite leaf chamber, and measurements for each light level began when the CO₂ level in the chamber had reached 360 ppm, which was approximately the ambient CO₂ level in the plot at noon on a sunny day. A fan in the leaf chamber assisted in regulating leaf temperature, and both leaf temperature and humidity were monitored to ensure relative stability during the course of measurements. Leaf area was estimated by tracing the shape of the leaf in the chamber onto graph paper, cutting the shape out, weighing the sample, and converting the weight to area using a previously established weight:area ratio for the same paper. Light levels were controlled by means of screens placed between an artificial light source and the leaf chamber. A heat-reflective glass screen was also used between the light source and the chamber to avoid heat build-up in the chamber.

Leaflet length, leaflet width, and the basal circumference of the aerial shoot (the pseudostem diameter) were measured for each ramet in mid-June of 1995 following full leaf expansion. The relationship between photosynthetic rate and reproductive effort could not be investigated because only one female ramet produced mature fruits in 1995.

Data analysis. The light compensation point, apparent quantum yield, dark respiration rate, and light-saturated photosynthetic rate (A_{max}) for each individual were estimated by fitting a Michaelis-Menten equation (with dark respiration as the y intercept) to the raw data using Proc NLIN (SAS Institute, Cary, NC). These estimates were then analyzed for mean differences among males and females using the paired t-test procedure in Microsoft Excel. Differences in the fitted estimates of A_{max} , dark respiration, and quantum yield among gender and genotype were analyzed with a two-way Analysis of Variance using Proc GLM (SAS Institute, Cary, NC).

Leaflet length and width were summed to obtain a single measure of leaf size. To ensure that this single linear measurement provided an accurate reflection of leaf size, leaf areas of a subsample of thirty individuals randomly chosen from the common garden population were obtained using a hand-held leaf area meter (LiCor 3000A) and regressed against the sum of the leaf measurements ($R^2 = 0.964$, the regression was significant at the 0.050 level). This regression was used to scale the photosynthetic measurements up from a per area basis to the whole-plant level. Differences between males and females in the whole-plant photosynthetic rate were analyzed using the paired t-test procedure in Microsoft Excel. An Analysis of Covariance on photosynthetic rate with pseudostem diameter as a covariate and gender as a main effect, and regressions investigating the effect of pseudostem diameter on photosynthetic rate were performed using SYSTAT 7.0 for Windows (SPSS, Inc., Chicago, IL).

RESULTS

Paired t-tests suggest that males had a significantly higher light-saturated rate of photosynthesis ($7.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ vs. $5.73 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P = 0.050$) and a substantially higher light compensation point (7.67 vs. 2.26 , $P = 0.003$) than females. Neither dark respiration nor apparent quantum yield differed significantly between genders (Table 1). However, two-way analyses of variance of A_{max} , dark respiration, and quantum yield all revealed significant differences between the genders, as well as significant differences among genotype (Table 2) for all three points on the light curve. Figure 1 clearly shows that the males had a higher overall rate of photosynthesis compared with females. In

Table 1. Results of paired t-tests for differences among males and females of the same genotype. There were six degrees of freedom for each t-test conducted. Means are reported with standard deviations. Light compensation point and quantum yield were estimated by fitting a Michaelis-Menten equation to the raw photosynthetic data for each male and female ramet of all pairs of genotypes using Proc NLIN. The Whole Plant Photosynthetic Rate (WPPR) was calculated by scaling Amax up to the leaf area of each individual plant.

	Males $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Females $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	t-Test
Amax	7.32 ± 1.65	5.73 ± 1.09	$t = -2.44 P(T \leq t = 0.050)$
Light compensation point	7.67 ± 1.72	2.26 ± 2.48	$t = -4.65 P(T \leq t = 0.003)$
Quantum yield	0.07 ± 0.00	0.13 ± 0.10	$t = 1.22 P(T \leq t = 0.268)$
Dark respiration	0.53 ± 0.22	0.31 ± 0.32	$t = -1.33 P(T \leq t = 0.233)$
WPPR	1791.71 ± 204.13	3421.44 ± 352.86	$t = 3.15 P(T \leq t = 0.010)$

Table 2. Results of two-way Analyses of Variance for differences among gender and genotype. Quantum yield estimated by fitting a Michaelis-Menten equation to the raw photosynthetic data for each individual measured using Proc NLIN.

	Model R ²	Source of Variation	df	MS	F	P
Amax	0.794	Genotype	7	23.605	37.53	0.0001
		Gender	1	82.115	130.55	0.0001
Quantum yield	0.516	Genotype	7	0.034	13.28	0.0001
		Gender	1	0.065	25.33	0.0001
Dark respiration	0.477	Genotype	7	0.367	9.24	0.0001
		Gender	1	1.552	39.06	0.0001

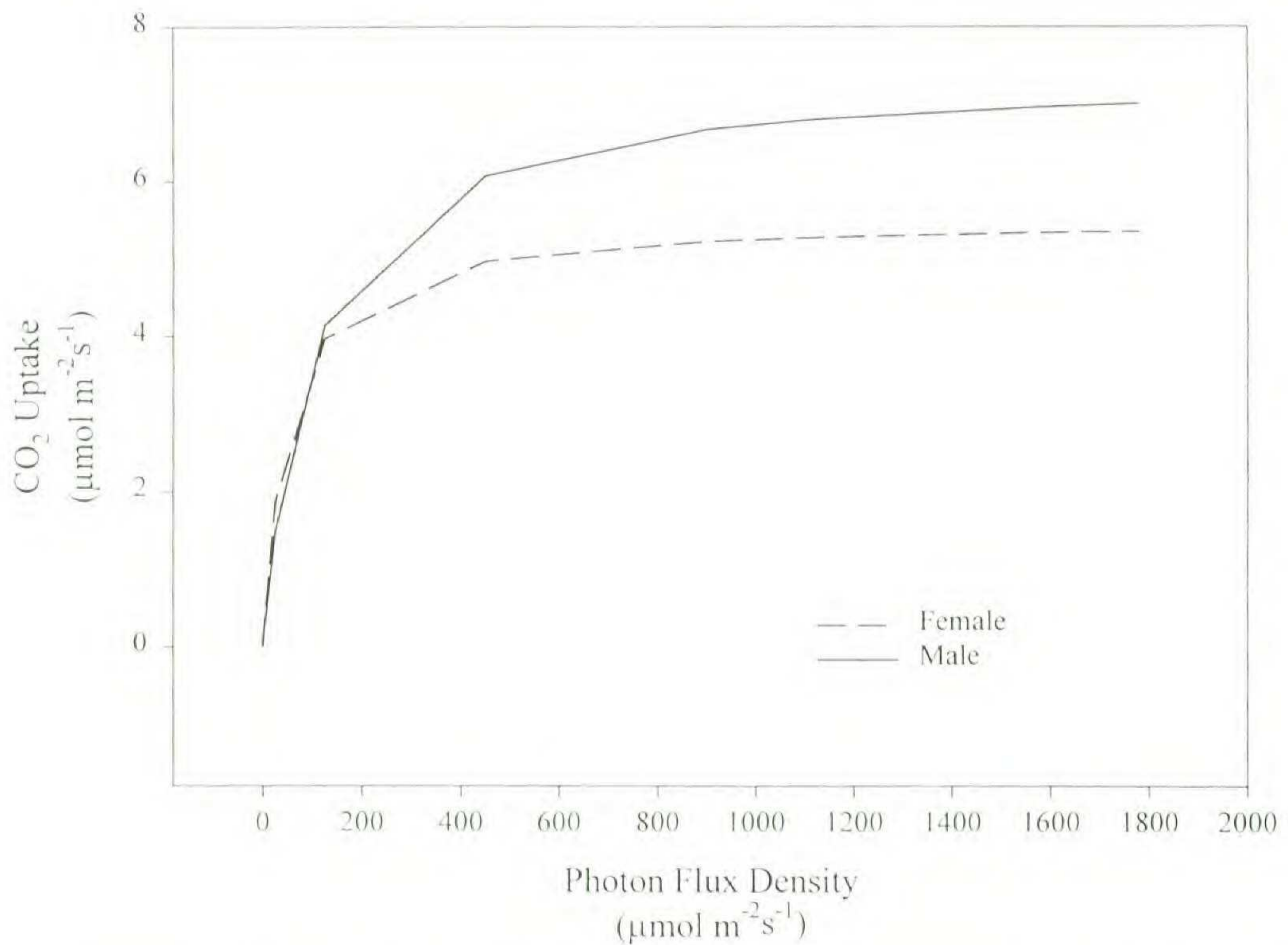


Figure 1. Photosynthetic light response curves averaged across all males (solid line) and all females (dotted line). Values for the curve were obtained by calculating the averages for the maximum rate, A_{max} , light compensation point, apparent quantum yield, and dark respiration.

one pair of clones, however, the female had a higher photosynthetic rate than the male of the same genotype. This female did not fruit. Gender and genotype together describe 79.4% of the variation in A_{max} and 51.6% of the variation in quantum yield, but only 47.7% of the variation in dark respiration.

At the whole-plant level, females had a significantly greater carbon gain than did males, in spite of a lower maximum rate of photosynthesis on a per unit area basis because of their much greater leaf area (Table 2). Total leaf area of males included in the study was $249.26 \text{ cm}^2 \pm 78.2$, while the total leaf area of females included in the study was $611.11 \text{ cm}^2 \pm 189.606$ (means reported with standard deviations). A regression between photosynthetic rate per unit area and pseudostem diameter for females only revealed a significant inverse relationship (Figure 2). Overall, the effect of gender on photosynthetic rate per unit area was no longer evident after controlling for pseudostem diameter (Table 3).

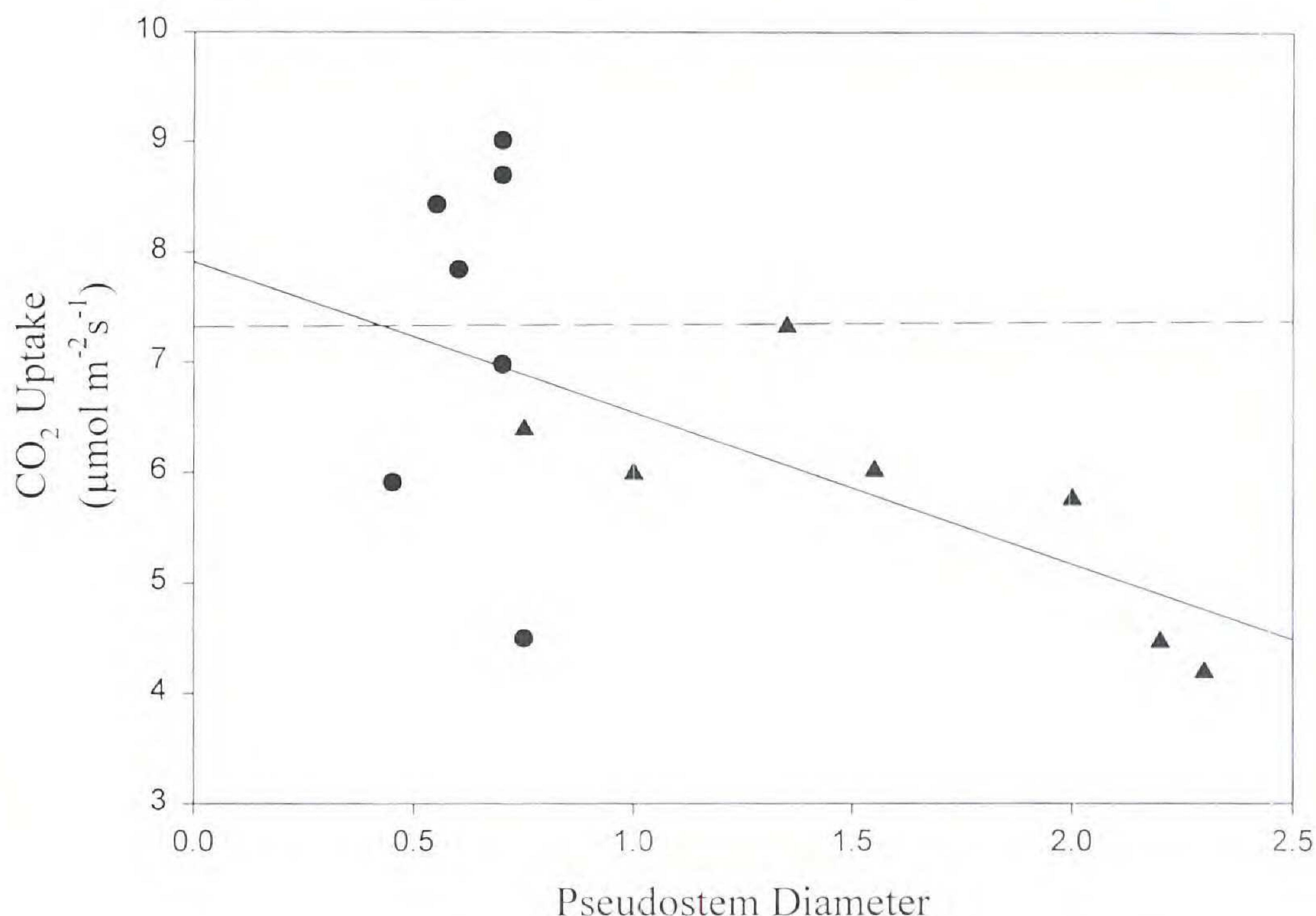


Figure 2. Regressions of photosynthetic rate (CO_2 uptake) and pseudostem diameter (cm). Males: $y = 7.326 + 0.020x$ ($F_{1,6} = 0.0$; $P = 0.998$; $N = 7$; $R^2 = 0.0$). Data points for males are shown as solid circles and the regression line is dashed. Females: $y = 7.913 + -1.368x$ ($F_{1,6} = 6.641$; $P = 0.05$; $N = 7$; $R^2 = 0.570$). Data points for females are shown as solid triangles and the regression line is solid.

Table 3. Results from the Analysis of Covariance with photosynthetic rate as the response variable, gender as a main effect and pseudostem diameter as a covariate. Adjusted Least Squares (LS) means for female and male photosynthetic rates also reported; these represent the photosynthetic rate when adjusted by the covariate.

Source of Variation	SS	df	MS	F	P
Gender	0.162	1	0.162	0.091	0.768
Pseudostem diameter	3.908	1	3.908	2.207	0.166
Error	19.484	11	1.771		
Adjusted LS					
	Mean	SE	N		
Female	6.368	0.660	7		
Male	6.704	0.660	7		

DISCUSSION

Bateman's principle suggests that female reproductive success is limited by resources while male reproductive success is limited by mate availability (Bateman 1948). As a result, males and females are expected to have different patterns of reproductive allocation, with female reproduction incurring greater costs. Many morphological, physiological, and life history traits appear to have become divergent among the sexes of dioecious species in response to differential reproductive costs. It has been suggested that females of dioecious species might have higher photosynthetic rates relative to males of the same species (reviewed in Dawson and Geber 1999; Delph 1999) as differences in the assimilation rates of males and females may arise as a result of increased sink strength in females, driven by maturing embryos and fruits (Dawson and Bliss 1989; Delph 1999; Delph and Meagher 1995).

Arisaema triphyllum has many traits in common with dioecious species for which females are known to have higher reproductive costs relative to males. In particular, larger females produce more flowers, fruits, and seeds than smaller females (Lovett Doust et al. 1986); females devote a greater portion of dry weight to reproductive structures than do males (Lovett Doust and Cavers 1982); and females have a higher mortality rate than males (Policansky 1987). Therefore it was reasonable to hypothesize that females in this species would have a greater photosynthetic capacity than males. However, the results presented above differ significantly from the general expectation that females will exhibit a higher maximum rate of photosynthesis than males (Dawson and Bliss 1989; Dawson and Ehleringer 1993). Males of *A. triphyllum* had significantly higher photosynthetic rates than females of the same genotypes on a per unit area basis.

These results are consistent with other recent studies in which males had higher rates of photosynthesis than females (Gehring and Monson 1994; Laporte and Delph 1996; Marshall et al. 1993; Nicotra 1997). Marshall et al. (1993) have suggested that the sheer number of gametes produced by males may offset the apparent higher cost of female gametes, thus giving rise to a higher overall cost for males. This might then lead to selection for higher photosynthetic rates among males. In *Arisaema triphyllum* photosynthetic rates in males were not correlated with corm size

(measured as pseudostem diameter), therefore it seems likely that current demands for resources may be a sink for males. This raises the possibility that males may have higher reproductive costs than previously expected, and that the higher photosynthetic rates are a response to these demands. It must be pointed out, however, that total carbon acquisition by females far exceeded that of males.

Gehring and Monson (1994) have suggested that leaf nitrogen levels play an important role in determining rates of photosynthesis. In their study, males had higher leaf nitrogen levels than the females, as well as higher photosynthetic rates. They conjectured that females translocate leaf nitrogen to the developing fruits, thereby limiting local photosynthetic rates in the leaves. Nicotra (1997) reported similar results; males in the dioecious species *Siparuna grandiflora* Perkins had higher leaf nitrogen levels, and exhibited higher photosynthetic rates than females that were maturing fruits. In contrast, males of *Phoradendron juniperinum* had higher photosynthetic rates, but there were no differences in leaf nitrogen levels (Marshall et al. 1993). Overall, these findings raise the question: how do females meet the estimated two-fold increase in resource demand for reproduction when they have lower photosynthetic rates? In *Arisaema triphyllum*, greater female size is most likely a response to the greater overall carbon demand that must be met, but at reduced photosynthetic rates. This is consistent with the current finding that as female size increases, photosynthetic rates decrease, and also with the estimates of whole-plant carbon gains that are so much greater for females, as a result of their greater size relative to males of the same genotype.

As the growing season progresses, and carbon demands from maturing embryos and developing fruits increase, the relative photosynthetic rates of males and females may be quite different. Measuring photosynthetic rates throughout the growing season would no doubt yield interesting evidence regarding differential carbon acquisition and allocation patterns among males and females of this species. For example, Nicotra (1997) found that during flowering, females had greater photosynthetic rates, while males exhibited higher rates later during fruit maturation. Although in *Silene latifolia*, males had consistently higher photosynthetic rates than females, while females maturing fruits had

higher rates than females without fruits (LaPorte and Delph 1996).

Genetic differentiation in photosynthetic capacity has been shown between populations (Teramura and Strain 1979; Winn and Evans 1991) and among genotypes (Kuiper and Smid 1985), as well as among family lines (Geber and Dawson 1990). For the individuals studied here it appears that sexual dimorphism in this trait may be influenced by genotype. Average differences among the sexes of dioecious species may mask substantial variation at the individual level. It is possible for the average difference between males and females to be statistically significant (Figure 1), while individual pairs show underlying variation at the same time (Table 2). Thus, the average performance of males and females in a population sample may depend strongly on how representative the individuals chosen for study are of the population as a whole.

Photosynthetic rates in this experiment were measured at or just after flowering to measure carbon acquisition when males and females were supporting similar loads of reproductive tissue (i.e., pedicels, inflorescences, and the bracteolate spathe characteristic of this family). Recent investigations into another aspect of this species' biology, notably the timing of developmental events critical to reproduction, have shown that in addition to maturing and maintaining the current year's reproductive tissues, individuals were also initiating reproductive structures for the next year (Vitt 1997). In effect, plants were assessing, and presumably responding to, both their current and future costs of reproduction simultaneously.

Males in this species senesce earlier in the season than females (Vitt 1997), and it may be that higher rates of photosynthesis have evolved concurrent with the male phase to compensate for the shorter period of carbon assimilation. The underlying mechanism remains a mystery, however there are at least two possibilities. First, as Gehring and Monson (1994) have noted, females may translocate nitrogen to developing seeds, leaving males with a higher leaf nitrogen content allowing them higher photosynthetic rates. In this study, however, photosynthetic measurements were taken at the time of flowering in an effort to control for embryo sink strength. A second possibility is that males may be translocating photosynthate to the corm at a rate exceeding that of females.

The corm is a sink for photosynthate, providing storage for carbon that is assimilated over and above current reproductive and maintenance costs. Corm weight has been significantly correlated with pseudostem diameter ($R^2 = 0.998$, $P = 0.004$; Vitt 1997). Because of the close association of the corm and the pseudostem, physically as well as statistically, pseudostem diameter is a good measure of a plant's current resource status and has been found to be the best overall predictor of current gender (Vitt 1997). Individuals with a smaller pseudostem diameter were male, and the probability of expressing as a female increased with increasing pseudostem diameter.

A regression that included only females revealed a significant inverse relationship between pseudostem diameter and photosynthetic rate; as corm size increased, the photosynthetic rate decreased (Figure 2). There was no relationship between these traits for the males included in this study. While there was some variation in photosynthetic rate among males, there was very little variation in pseudostem diameter, while females had a large variation in pseudostem diameter (Figure 2). The evidence suggests the corm is not as strong a sink for very large females, which have greater stored resources, at least during the flowering phase of the growing season. This conclusion is supported by the Analysis of Covariance reported in Table 3, which shows that the effect of gender on photosynthetic rate is greatly reduced after controlling for pseudostem diameter, and is not significant at the 0.09 level. It must be noted, however, that size and sex expression are tightly correlated in this species making it difficult to determine the separate effects of these variables.

Corm size, and thus sink strength, was affecting leaf-level photosynthetic rates, at least in females. This is consistent with the findings of Laporte and Delph (1996), who found similar patterns in leaf-level photosynthetic capacity. Photosynthetic rates in *Arisaema triphyllum* appeared to be sink-limited in females at the time of flowering, while this did not appear to be the case for males. Males in *A. triphyllum*, despite their lower whole-plant assimilation rate, appeared to use the net carbon gain to change gender in the next growing season. Males had a greater probability of becoming female in the subsequent growing season than females had of remaining female (Vitt 1997). Overall, males and females appeared to have different patterns of carbon assimilation, at least very early in the growing season.

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